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Changes in belowground biomass after coppice in two *Populus* genotypes

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ABSTRACT

Despite the potential of high-density, short-rotation woody biomass plantations to sequester carbon (C) in the soil, few studies have examined their belowground components. We were particularly interested in the biomass allocation patterns after the change from a single-stem (pre-coppice) to a multi-shoot (post-coppice) system, as well as in the fine root (Fr; ∅ < 2 mm) mortality after coppice for their implications in the belowground C cycle. The root system of selected trees from two poplar (*Populus* spp.) genotypes – Skado and Koster – were excavated for the determination of coarse (Cr, ∅ > 5 mm) and medium-sized (Mr, ∅2–5 mm) roots. After two 2-year rotations, the Cr biomass (dry mass, DM) was higher in the *P. trichocarpa* × *P. maximowiczii* genotype Skado (187.0 g DM m^{-2}) than in the *P. deltoides* × *P. nigra* genotype Koster (155.4 g DM m^{-2}). Both genotypes showed a relatively shallow, but extensive root system. Allometric equations were fitted between DM of Cr and Mr, and basal area. The root:shoot ratio decreased exponentially with basal area, showing the same trend for single-stem and multi-shoot trees. The soil coring technique was used to determine Fr mass at different dates and at different soil depths. The highest Fr biomass was detected in the upper 15 cm of the soil; no genotypic differences in Fr mass were detected at any soil depth. After coppice Fr mortality was significantly increased and weed root biomass significantly reduced. The coppice of the aboveground stems and shoots resulted in a high input of C into the soil and a large amount of C was stored in belowground tree biomass.

1. Introduction

Within the framework of the search for renewable (bio-)energy sources fast-growing trees such as poplars (*Populus* spp.) are being intensively studied, in particular because of the potential use of their biomass and as a management option to sequester carbon (C) in the soil (Smith, 2004). In a short-rotation woody crop (SRWC) poplars are harvested and coppiced every two to five years and the produced woody biomass is converted into bioenergy. Several ecological, physiological and genetic aspects of SRWC have been examined to further improve its biomass yield (King et al., 1999; Dickmann et al., 2001; Laureysens et al., 2005). Within this framework there is a particular interest in selecting species or genotypes that prioritize allocation of biomass to harvestable and economically valuable organs (i.e. stems, branches). This implies a reduced allocation of biomass to roots. Although the belowground parts are crucial for woody biomass production and C sequestration in the soil, there are disproportionally few studies on these tree organs.

Because of their high fine root turnover (Block et al., 2006), intensively managed poplars under SRWC regime might have a high potential for C sequestration in the soil. At the end of each (short) rotation the trees are harvested at the base of their stump, resulting in the regeneration of multiple new shoots from the stump and from the roots (multi-stem coppice system). Different simulation models for poplar SRWC assume a mortality of all fine roots (Fr) after the coppice of the aboveground biomass (Garten et al., 2011; Werner et al., 2012). This confers a huge input of C into the soil after coppice, and it presents an important control on soil C sequestration (Garten et al., 2011). This assumption has, however, never been validated empirically. A recent study on oaks showed that forest interventions often result in an increase of Fr mortality and in a reduction of Fr biomass (Ma et al., 2013). Only a few studies have addressed the effect of the total aboveground removal on the vertical and the temporal distribution of fine roots, in particular on the annual production and turnover rate (Dickmann et al., 1996; Dipesh and Schuler, 2013). In case all Fr would die after the harvest, this would result in a tremendous C input into the soil and it should be reflected in larger C stocks in the soil. Recent empirical research, however, has indicated that poplar SRWC did not increase the C stock in the soil (Walter et al., 2014).

A SRWC potentially not only sequesters C into the soil, but also in the belowground biomass (Pacaldo et al., 2014). The below-

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ground organs such as the stump, coarse roots (Cr) and Fr remain in the soil after coppice, and also contribute to the C sequestration. Moreover, the allocation of C belowground and its partitioning over different root compartments (Cr and Fr) and soil depths are important controls of the soil C sequestration (Jandl et al., 2007; Franklin et al., 2012). This C sequestration potential could also be influenced by the initial soil C and nutrient contents of the former land use. Within the framework of SRWC we were particularly interested in the effects of the removal of aboveground biomass through coppice on: (i) the seasonal and the vertical dynamics of Fr biomass and necromass, (ii) the C allocation patterns over Fr and Cr, and (iii) the C sequestration potential of the belowground organs of two contrasting *Populus* genotypes. Within this context our hypotheses were: (i) harvesting of aboveground biomass decreases Fr productivity and increases Fr mortality in trees; (ii) the root:shoot ratio changes when trees are coppiced and change from a single-stem to a multi-shoot culture; (iii) the former land use (cropland or pasture) influences the belowground traits. The answers to these two hypotheses are analyzed within the context of a higher soil resource use efficiency and of the potential of SRWC for C sequestration.

2. Materials and methods

2.1. Experimental site

The experimental field site of this study is located in Lochristi, Belgium (51°06′N, 03°51′E), at an altitude of 6.25 m above sea level with a flat topography, and consists of a high-density SRWC plantation with poplar (*Populus*). The long-term average annual temperature at the site is 9.5 °C and the average annual precipitation is 726 mm (Royal Meteorological Institute of Belgium). The region of the field site is pedologically described as a sandy region with a poor natural drainage. The total area of the site is 18.4 ha. The former land-use types were (i) cropland (ryegrass, wheat, potatoes, beets, and most recently monoculture corn with regular nitrogen (N) fertilization at a rate of 200–300 kg ha^{-1} y^{-1} as liquid animal manure and chemical fertilizers), and (ii) extensively grazed pasture (Fig. 1; left panel). For more information on the site and the planting scheme, see Broeckx et al. (2012). A detailed soil analysis was carried out in March 2010, prior to planting. The analysis characterized the soil type as a sandy texture. In the upper soil layer, C and N concentrations were significantly lower in cropland as compared with pasture and decreased exponentially with depth in both former land-use types (Table 1). More details on soil analyses have been provided by Broeckx et al. (2012) and Verlinden et al. (2013a,b).

After initial soil sampling and site preparation, 12 *Populus* spp. genotypes – including pure species as well as interspecific hybrids – were planted in monoclonal blocks in a double-row planting scheme on 7–10 April, 2010. Uniform hardwood cuttings of 24 cm length were used for the planting. The distance between tree rows was alternating 75 cm (narrow inter-rows) and 150 cm (wide inter-rows). The spacing between trees within a row was 110 cm, yielding an overall theoretical initial tree density of 8000 trees per ha. Within the 18.4 ha of the experimental site, a total of 14.5 ha was planted (Fig. 1; right panel). After one year, an overall average mortality of 18.2% was observed on the plantation (Broeckx et al., 2012). Re-planting with one-year old rooted plantlets reduced the mortality to a plantation average of 15%. The site has been managed as an operational SRWC plantation, in two-year rotation cycles, for two rotations (four years in total; 2010–2014). A first harvest was carried out on 2–3 February 2012, followed by the onset of the second rotation which finished with the second harvest on 18–20 February 2014. Manual and chemical weed controls were applied during the first and the second year – of the first rotation – consistent with conventional SRWC operational management (Ledin and Alriksson, 1992). Despite the different weed control measures during the first rotation, common agricultural weeds remained abundant within the plantation, including thistles (*Carduus* spp., *Circium* spp.), *Urtica* spp., *Capsella bursa-pastoris* L., *Convolvulus* spp., *Matricaria chamomilla* L., *Taraxacum officinale* Weber and various Gramineae species. As nutrients and water were not limiting at the site (Broeckx et al., 2012), no fertilization or irrigation were applied during the study. A more detailed description of the plantation lay-out, management and plant materials used, can be found in Broeckx et al. (2012) and in Berhongaray et al. (2013a).

2.1.1. Climatic data

The experimental site is equipped with eddy covariance technology to monitor net fluxes of various gases (Zona et al., 2013). A LI-7000 fast response gas analyzer (LiCor, Lincoln, USA) was used to continuously measure latent heat from air samples at the eddy covariance mast from June 2010 onwards. Latent heat flux was converted into evapotranspiration using air temperature and latent

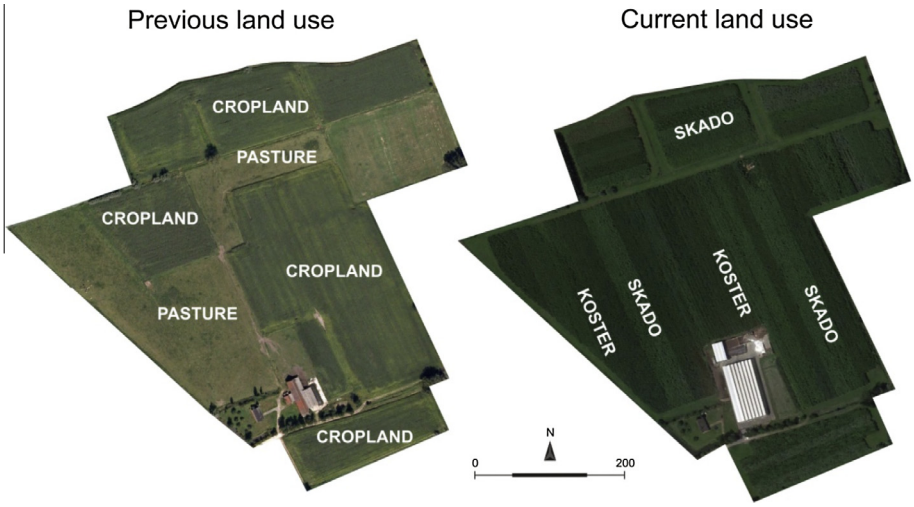

Fig. 1. Aerial image of the field site before and after the establishment of the SRWC. The map on the left shows the distribution of the previous land-use types, i.e. pasture land and cropland. The map on the right shows the monoclonal blocks indicating the location of the genotypes Skado and Koster. (Source: Google Earth).

Table 1
Soil bulk density, pH and carbon-nitrogen (C/N) ratio of the soil layers on both previous land-use types (adapted from Broeckx et al., 2012).

Soil property	Depth	Pasture	Cropland
pH	0–30 cm	5.12 (±0.167)	5.47 (±0.135)
	30–60 cm	5.64 (±0.160)	5.87 (±0.280)
C:N	0–30 cm	11.08 (±0.238)	12.17 (±0.241)
	30–60 cm	13.11 (±0.841)	14.85 (±0.874)
Bulk density [g cm^3]	0–30 cm	1.360 (±0.009)	1.444 (±0.009)
	30–60 cm	1.504 (±0.014)	1.492 (±0.011)

heat of vaporization. Precipitation was monitored from June 2010 onwards using a tipping bucket rain gauge (model 3665R, Spectrum Technologies Inc., Planfield, USA) installed next to the eddy covariance mast. The soil water balance was calculated as the difference between the monthly cumulative precipitation minus the monthly evapotranspiration, considering positive values as water excess and leaching (Fig. 2).

2.2. Data collection in the field

The samples for the present study were collected during the single-stem system of the first rotation (2010–2011) and the multi-stem system of the second rotation (2012–2013) of the plantation. Due to the high labor intensity with belowground analyses, this study was restricted to two genotypes with a contrasting aboveground habitus, i.e. Koster (*P. deltoides* Bartr. (ex Marsh.) × *P. nigra* L.) and Skado (*P. trichocarpa* Torr & Gray (ex Hook) × *P. maximowiczii* Henry). Both genotypes were selected as being the most representative for the plantation based on their parentage, origin and area coverage in the plantation (Broeckx et al., 2012). The crown structure of Koster was described by the breeder (Buiteveld, 2007) as 'closed, broad pyramidal crown with thin branches'. Although this description was based on low-density, single-stem trees, it was confirmed in our high-density SRWC plantation. No such breeder information was available for Skado, but from our observation we could describe Skado as having a deeper, more narrow crown (difference in height growth), with fewer, heavier branches. The main characteristics (less and taller shoots in Skado after coppice) still held after coppice in the multi-shoot system. The crown architecture of both genotypes was described in detail and discussed in Broeckx et al. (2012) and Verlinden et al. (submitted September 2014). Samples were collected on both previous land-use types, i.e. cropland and pasture.

2.2.1. Medium-sized roots, coarse roots and stump

Belowground woody biomass was determined by excavation of the root system and the stump immediately after each of the two harvests. In February 2012, five single-stem trees of different stem diameters (from 20 mm to 60 mm at 22 cm height above the soil) were selected from each genotype (Koster and Skado) and for each of both former land-use types (20 trees in total). In February 2014, four multi-shoot trees with a different number of shoots were selected and excavated, for genotype Koster on both former land-use types, but for genotype Skado only on the former cropland land use (16 multi-shoot trees in total). All shoots from each tree were counted and their diameter was measured at 22 cm height above the insertion point. Basal areas were calculated from tree stem and shoot diameter measurements (see further below). In both excavation campaigns, the remaining stumps (Stu) and roots were excavated from a Voronoï polygon (Razakamanarivo et al., 2012) confined by an area of 1.1 m × 1.125 m (planting distance in the rows × sum of half inter-row distances). All roots within this area were collected, assuming that roots from adjacent trees compensated for roots of the selected tree growing outside the sampled area. The excavation depth was limited to 60 cm, as very few roots were observed below 60 cm (see Results section further below). Roots that penetrated below 60 cm during the excavation were not recovered by complete excavation, but were pulled out of the soil. Coarse roots (Cr; ∅ > 5 mm) and medium-sized roots (Mr; ∅ = 2–5 mm) were collected separately in the 0–15 cm and 15–60 cm soil layers from both the narrow and the wide inter-rows. Total dry biomass of these roots (Cr and Mr) and of the remaining 15 cm high stump was determined after oven drying at 70 °C in the laboratory. Since no significant effect of genotype or of former land-use type was found, all data were pooled (see Results section further below). Dried root mass was ground for subsequent C and N analyses. An average of the C mass fraction of all samples per root class was used to calculate the belowground woody C pool. Belowground biomass values at the tree level (i.e. Mr and Cr) were scaled up to the plantation level by using the specific planting density and mortality of each plot. The same approach was used for the aboveground components as explained further below.

2.2.2. Fine roots

The soil coring technique was used to determine fine root (Fr; ∅ < 2 mm) biomass (Berhongaray et al., 2013a). Three sampling strategies were applied: (i) a high frequency sequential core sampling at 0–15 cm to monitor Fr temporal dynamics during the years before and after the first harvest (coppice); (ii) a sampling at different depths before and after the first harvest; (iii) a low frequency

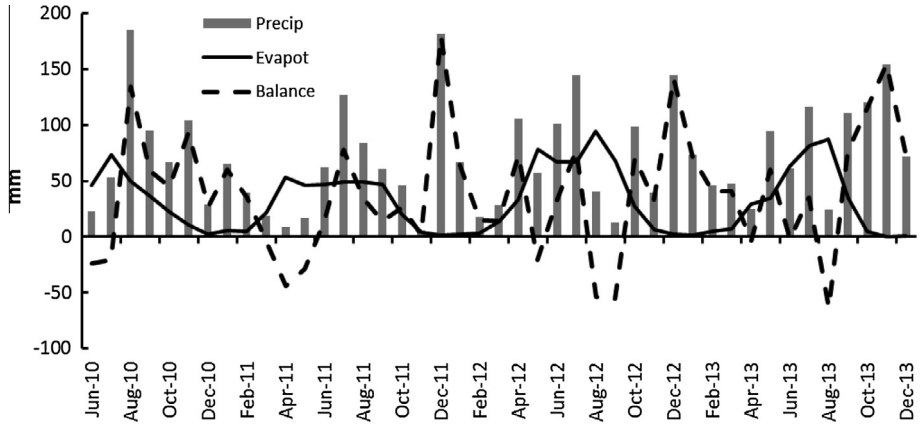

Fig. 2. Course of the monthly precipitation, evapotranspiration and water balance during the four years of the two rotations of the study in Lochristi (Flanders), Belgium. No data were available before 30 May 2010. The water balance was calculated as precipitation – evapotranspiration.

sampling to look at the differences between the former land-use types. The two first mentioned approaches (i) and (ii) were applied for both genotypes, while the third approach was only applied for genotype Skado. At each sampling campaign, an 8 cm diameter × 15 cm deep hand-driven corer (Eijkelkamp Agrisearch equipment, The Netherlands) was used (cfr. Oliveira et al., 2000). The number of samples differed at each sampling campaign and at each depth depending on the expected intrinsic variability of the Fr mass. Based on our previously described approach and methodology (Berhongaray et al., 2013b), the number of replicates per treatment (combination of genotype and land-use type) varied from 12 in winter to 20 in summer, and from 20 in the upper soil layers to 10 in the deeper layers. Three approaches were used to quantify Fr mass.

(i) Sequential soil coring was used to determine Fr mass, Fr production and Fr mortality for the second growing season of the first rotation (i.e. 2011) and the first growing season of the second rotation (i.e. 2012), i.e. the year before and the year after the first coppice. From February 2011 till November 2012 the upper 15 cm of soil layer was sampled every 2–3 weeks, except for the winter when the sampling intensity was decreased. During 2011, 20 samples were collected at every sampling campaign for each genotype. During 2012, the number of samples was different at each sampling date, following the expected intrinsic variability of the Fr biomass based on the experience of the previous growing season (i.e. 2011). At each sampling campaign in 2011 and in 2012, half of the samples were collected in the narrow and half in the wide inter-rows, randomly distributed over the planted area within the former pasture.
(ii) A soil core sampling at different depths was performed in August 2011 and August 2012. In August 2011 sampling was performed in six different soil layers (0–15 cm, 15–30 cm, 30–45 cm, 45–60 cm, 60–75 cm and 75–90 cm), whereas in August 2012 four different soil layers (0–15 cm, 15–30 cm, 30–45 cm and 45–60 cm) were sampled.
(iii) A low frequency sampling was performed to compare the effect of the previous land use on the seasonal dynamics of Fr. Soil samples from the top 15 cm were collected from genotype Skado in spring (May 2011) and summer (August 2011) of the first rotation as well as in winter (February 2012), spring (May 2012) and summer (August 2012) of the second rotation. Immediately after collection in the field, all samples were transported to the laboratory and stored in a freezer until processed.

Fine roots were picked from each sample by hand while: (a) separating weed roots (Wr) from poplar roots, (b) sorting poplar roots in dead and living roots, and (c) sorting Fr in two diameter classes: 0–1 mm and 1–2 mm for independent Fr productivity and mortality calculations of each diameter class (see below for more details). Poplar roots were sorted from Wr based on morphological characteristics. Poplar roots showed a brown color and a dense ramification pattern, while Wr had a lighter color and less ramification. The sorting of dead (necromass) and living Fr was based on the darker color and the poorer cohesion between the cortex and the periderm of the dead roots (Janssens et al., 1999). After washing, fine roots were oven dried at 70 °C for 1–4 days to determine the dry root mass. Fr mass of one core sample picked for x min (i.e. 5–20 min) was converted into total Fr mass in the sample (i.e. after 60 min picking duration) using Richard's equation (as explained in detail by Berhongaray et al. (2013b)) and expressed in g DM m^{-2}. Subsamples of dried Fr were ground for further C and N-analyses. More details on Fr collection and data processing can be found in Berhongaray et al. (2013a, b).

2.2.3. Aboveground biomass

The aboveground woody biomass was calculated for both genotypes from previously published data for the first rotation (Verlinden et al., 2013b) and from new measurements for the second rotation. A detailed inventory of stem and shoot diameter (D) distribution and of mortality was carried out for each genotype at the end of each rotation in December 2011 and December 2013. The number of shoots per tree was counted, stem and shoot diameter at 22 cm above the soil was measured for one entire row per monoclonal block and the number of missing trees was counted. Based on the stem diameter distribution of the plantation, ten trees of each genotype were selected for destructive harvest, covering the widest possible range of number of shoots and of stem and shoot diameter. Stem and shoot diameter at 22 cm was measured on the selected trees with a digital caliper (model CD-15DC, Mitutoyo Corporation, Japan, 0.01 mm precision), before the tree was harvested. The tree was harvested at 7 cm above soil level in the first rotation and at the insertion point in the second rotation. After determination of dry mass (DM) of each stem, allometric relationships were established between stem or shoot diameter and aboveground dry mass, fitted as $DM = a \cdot D^b$ for both genotypes, with a and b as regression coefficients (Broeckx et al., 2012).

2.2.4. Carbon and nitrogen analysis of biomass samples

Root samples were analyzed for their C and N mass fractions by dry combustion using a NC-2100 element analyzer (Carlo Erba Instruments, Italy). Root mass was converted to C mass using the average root C mass fraction, and expressed in g C m^{-2}.

2.3. Data analysis

2.3.1. Fine root production and mortality

For 2011 and 2012, Fr production (P) and mortality (M) were calculated using the "decision matrix" approach (Fairley and Alexander, 1985). The values of P and M were calculated separately for each Fr diameter class (i.e. 0–1 mm and 1–2 mm) and then added on each sampling date. All differences in biomass and necromass were taken into account during the calculation, assuming that the living and dead pools were continuously changing. This approach was better than using the significant differences between root mass of consecutive sampling dates, especially in the case of high-frequency sampling (Brunner et al., 2013), such as in our sampling campaign. For the calculation of the annual P, the productivity values from all sampling periods were summed from the beginning till the end of the year. More details on the calculation of root productivity and on the comparison of different methods to assess P can be found in Berhongaray et al. (2013a).

2.3.2. Allometric relationships

Allometric equations were used to scale-up belowground woody biomass components based on measurements of basal area (BA). The BA of each tree was calculated as $BA = \Sigma(\pi^*(D_i/2)^2)$, the sum of the calculated area of all the shoots (D_i = diameter of each individual shoot) for each selected tree. All stem or shoot diameters, and all BAs refer to measurements taken at a height of 22 cm above the soil. Stu, Cr and Mr biomasses were plotted against BA and allometric linear equations were fitted. The most reliable equations with higher determination coefficients (R^2) were selected. Average belowground woody root biomass (Cr and Mr) and stump biomass pool were estimated from the allometric equations and the full stem diameter inventory of each sampling year, made up in winter 2011–2012 and in winter 2013–2014.

2.3.3. Root:shoot ratio

The root:shoot ratio is commonly defined as the root biomass divided by the shoot biomass. The distinction between 'root' and

'shoot' is generally made at the ground surface level: the term 'root' refers to all biomass below the ground surface and 'shoot' represents all biomass above the ground surface. In the present study, the root:shoot ratio was calculated using woody biomass only (Cr, Mr, Stu, stem and branches), and excluding Fr and leaves. As the studied trees were planted in a SRWC plantation, we considered the harvesting height as the upper limit for the belowground biomass, instead of the ground surface. The belowground biomass was defined as all what remained in the field after the mechanical harvesting, and the aboveground as the biomass that is frequently harvested.

2.3.4. Statistical analysis

For root mass data at different depths a two-way Multivariate Analysis of Variance (MANOVA) was performed using land-use or season, as appropriate, and genotype as fixed factors, and the different depths as repeated measurements. The multivariate approach to the analysis of repeated measurements was used as it does not assume any particular model covariance between the repeated measurements. The hypotheses tested in an analysis of repeated measurements with treatment factor by grouping observations were: (i) there is no interaction between depth $*$ treatment, (ii) there is no effect of depth, and (iii) there is no treatment or group effect. In the case of a significant treatment effect, pairwise comparisons were performed using a Hotelling post-hoc test ($P \leqslant 0.05$). A second analysis was carried out partitioning the data in different sampling depths. In this case a two-way analysis of variance (ANOVA) was performed using land-use type and genotype as fixed factors, with inclusion of their interactions, for each sampling depth. Two-way ANOVAs were performed also using land-use type, genotype and their interactions as treatment factors, and different dependent variables such as C%, and plant density. In the case of a significant treatment effect, pairwise comparisons were performed using a Tukey post-hoc test ($P \leqslant 0.05$). The software *InfoStat* (Di Rienzo et al., 2011) was used for the analysis.

Although an optimal experimental design should include a control treatment without coppicing, it was not possible in our plantation and we also recognize that the establishment phase of the plantation is a special situation. This is the most critical period after the land use change of agriculture into SRWC. The herbaceous competition is one of the principal factors affecting the establishment, the success and the early productivity of the SRWC culture (with ecological and economic consequences). This has, however, been very poorly quantified in the literature, especially for belowground processes. The explicit quantification of the relative root productivity of the tree crop and the competing weeds is the principal contribution of the current study. It is, therefore, essential to characterize land use change effects early in the conversion from agriculture to SRC. Our presented data are useful for models that simulate long-term changes in relation to SRC.

3. Results

3.1. Fine roots

Biomass of Fr at a depth of 0–15 cm increased during the course of the second year of the first rotation (2011, pre-coppice, Fig. 3). There was no significant increase of Fr biomass, even a small reduction, in the first year of the second rotation (2012, post-coppice) just after the first harvest. Despite this small decrease in Fr biomass in 2012 (post-coppice), the Fr productivity was higher than the pre-coppice year (i.e. 2011). Necromass of Fr did not increase post-coppice as compared to pre-coppice (Fig. 3). The proportion of necromass remained rather low in both years, pre- and post-coppice; the necromass represented 6–11% of the total Fr mass. The Fr mortality increased significantly post-coppice. While Fr mortality was much lower than Fr productivity in 2011 (pre-coppice), it exceeded Fr productivity in 2012 (post-coppice).

In both genotypes the average Fr biomass and necromass significantly declined with increasing soil depth (Fig. 4). Using MANOVA, was shown that all soil depths biomass of Fr in the first year of the second year (2012; post-coppice) did not statistically differ from the second year of the first rotation (2011; pre-coppice). For genotype Koster, however, Fr biomass in the upper soil layer increased in 2012 (post-coppice) as compared to 2011 (pre-coppice; Fig. 4) when the data was partitioned by depth. For genotype Skado, Fr biomass was higher in the former cropland than in the former pasture (Table 2). No genotypic differences in Fr biomass were detected at any soil depth. The depth was a statistically significant factor in the MANOVA model. The highest Fr biomass was detected in the upper 15 cm. On average, Fr biomass in the upper 15 cm accounted for 63.6 ± 16.4 g DM m^{-2}. The Fr biomass in the upper

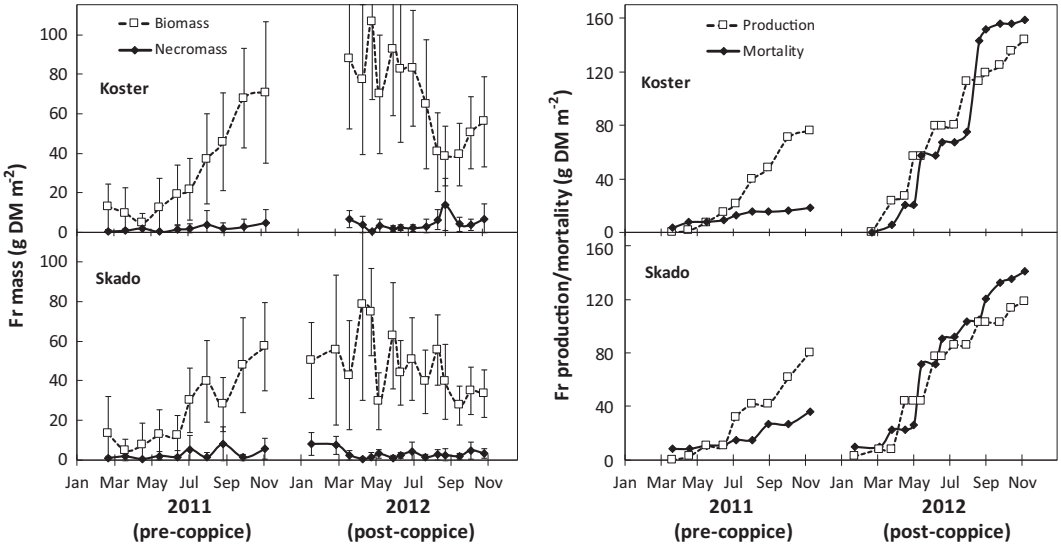

Fig. 3. Seasonal dynamics of fine root (Fr) biomass and necromass, and cumulated Fr production and mortality of two poplar genotypes the year before and after the first coppice, in February 2012.

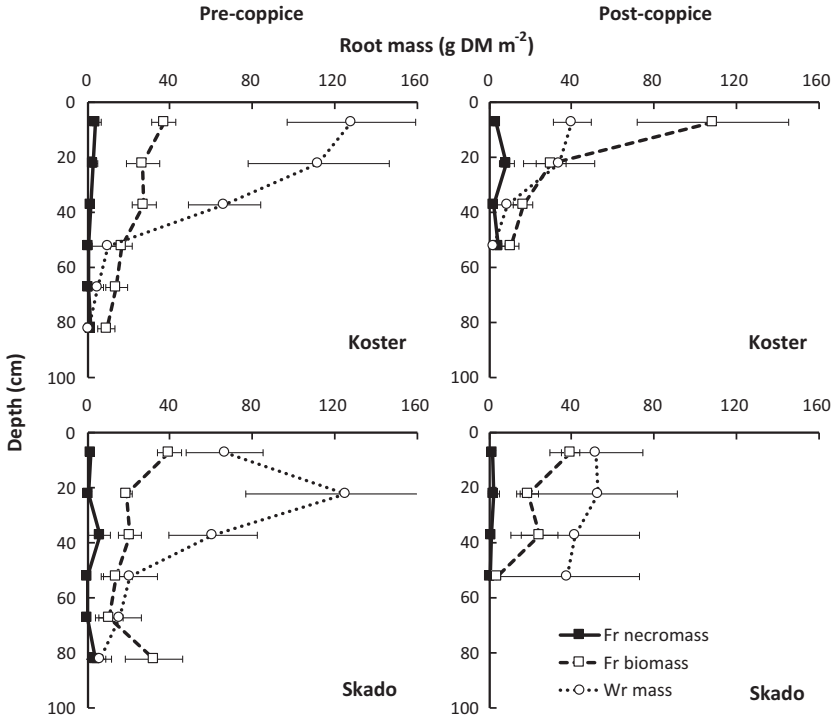

Fig. 4. Vertical distribution of fine root mass (∅ < 2 mm) of poplars and weeds under two poplar genotypes and for two consecutive years (2011 and 2012). Genotype Koster: top panels; genotype Skado: bottom panels. 2011: second year pre-coppice; 2012: first year post-coppice. Error bars indicate standard error of the mean; DM = dry mass; Fr = fine roots; Wr = weed roots.

Table 2
Fine root (∅ < 2 mm) biomass of poplars grown on two previous land use types (cropland and pasture). Mean values (± standard error) are presented. Significant differences (at $P \leqslant 0.05$) in the same row (sampling period) are marked with an asterisk (∗). 2011 = second year of the first rotation (pre-coppice), 2012 = first year of the second rotation (post-coppice). Mean (±SE); DM = dry mass; *n* = number of samples.

Season		*n*	Cropland (g DM m^{-2})	Pasture (g DM m^{-2})	Sig.
2011 (pre-coppice)	Spring	20	21.02 (±6.47)	7.28 (±3.21)	
	Summer	20	74.3 (±10.5)	43.36 (±6.96)	∗
2012 (post-coppice)	Winter	25	74.79 (±7.83)	52.62 (±5.52)	∗
	Spring	25	63.92 (±6.19)	60.82 (±13.5)	
	Summer	11	68.67 (±10.46)	39.87 (±4.51)	∗

15 cm of the soil represented 44.3% and 50.1% of the total Fr in the 0–60 cm profile of genotypes Skado and Koster, respectively.

In the second year of the first rotation (2011; pre-coppice), Wr biomass, mostly from grasses, was significantly higher than Fr of poplar in the upper 45 cm of the root profile. Overall, in 2011 the Wr showed a strong vertical distribution with a significant concentration in the upper 30 cm, while in 2012 (post-coppice) the Wr were more evenly distributed over the soil profile than the Fr.

3.2. Medium-sized and coarse roots

For trees of the same BA, no significant differences in Cr biomass were detected, neither between genotypes nor between previous land-use types. Consequently one single allometric equation was established at each sampling campaign to scale-up Cr biomass of the two genotypes across both previous land-use types using the BA frequency distribution (Fig. 5). It was, however, not possible to establish an allometric equation for Mr (Fig. 5). The up-scaled standing belowground woody biomass after both rotations significantly differed between both genotypes (Table 3). After the first rotation (pre-coppice), the Cr biomass was already higher in Skado (145.9 g DM m^{-2}) than in Koster (95.3 g DM m^{-2}). After coppice, the Cr biomass increased by 28% and by 63% to 187 g DM m^{-2} and 155 g DM m^{-2} for Skado and Koster, respectively Table 3.

The C concentration of the roots increased with root diameter class (Fr, Mr and Cr, Table 4). The C concentration was lowest (36% of C) in the Fr without significant differences between necromass and biomass. There were no significant genotypic differences in root C concentration. After the first rotation, most of the C was stored in the Cr, with 53.5 g C m^{-2}, followed by the Fr 40.1 g C m^{-2} and Mr 35.3 g C m^{-2}. The annual rate of C sequestration in the Cr averaged 18.4 g C m^{-2} y^{-1}. This annual rate was much larger in genotype Skado on the previous cropland, with 22.5 g C m^{-2} y^{-1}, than in the other land use and genotype, which averaged 17.0 g C m^{-2} y^{-1} (data not shown). The higher Cr for "Skado on previous cropland" per unit of land area (i.e. m^{-2}) compared to "Skado on previous pasture" could be explained by the lower tree mortality that resulted in a higher plant density per area (Table 3). The belowground woody biomass (Mr + Cr + Stu) increased by 30% after the first rotation. By the fourth year, the plantation had sequestered a total of 240 g C m^{-2} in belowground woody biomass. The Mr biomass remained constant between both sampling campaigns. The Mr biomass represented about 22% of the total root biomass.

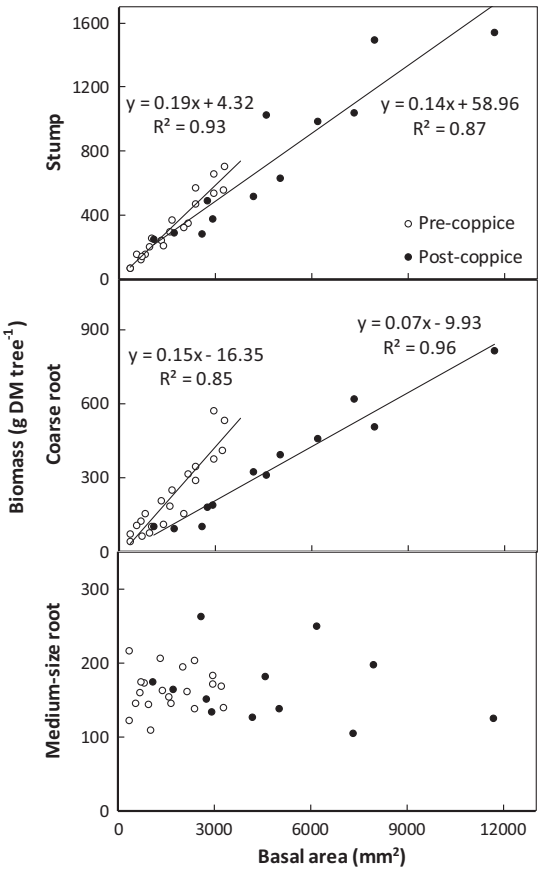

Fig. 5. Stump (top panel), coarse root (∅ > 5 mm; middle panel) and medium-sized root (∅ = 2–5 mm; bottom panel) biomass in the area occupied by a single tree (Voronoï polygon) in relation to its basal area (at 22 cm) on single-stem (2012) and multi-shoot (2014) trees. A linear equation was fitted to the allometric relationship between root biomass and basal area. Medium-sized root biomass was homogenously distributed over the basal area range, and no significant equation was fitted. DM = dry mass.

Table 4
Carbon (C) concentration (in %) of different belowground components. Wr = weed roots, Dr = dead fine roots (∅ < 2 mm), Fr = fine roots (∅ < 2 mm), Mr = medium-sized roots (∅ 2–5 mm), Cr = coarse roots (∅ > 5 mm), Stu = stumps. Different letters indicate significant differences in carbon concentration between different components (Tukey, $P < 0.05$). Mean (±SE); n = number of samples.

Root category	n	C%
Wr	179	30.4 (±0.38) a
Dr	103	35.9 (±0.61) b
Fr	334	36.6 (±0.31) b
Mr	28	42.0 (±0.40) c
Cr	50	42.3 (±0.30) c
Stu	20	43.5 (±0.51) c

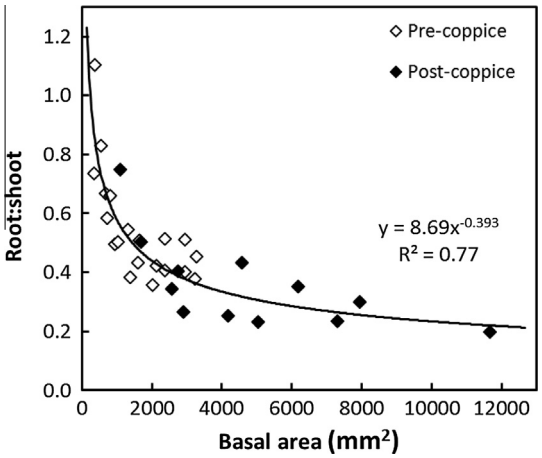

Fig. 6. The ratio of below- to aboveground biomass (root:shoot) in relation to tree basal area (BA) for the single-stem (2012) and multi-shoot (2014) trees, pre- and post-coppice respectively. Belowground biomass includes stump, coarse and medium-sized roots; aboveground biomass includes stem and branches. The equation was fitted using all the data from both years.

3.3. Root:shoot ratio

At the end of both rotations total (=above-plus belowground) standing woody biomass was higher in Skado than in Koster (Table 3). Although the aboveground biomass for genotype Skado was 23% higher than for Koster, there were no differences in the total belowground biomass. After the first rotation (pre-coppice), Cr and Mr represented 17% of the total standing woody biomass in Skado *vs.* 23% in Koster. This proportion of the total standing woody biomass dropped after coppice (i.e. in the second rotation) to 8.7% and 10.1% for Skado and Koster, respectively. In the first and in the second rotation, the Stu represented 14% and 12.5% of the total standing woody biomass in Skado *vs.* 16% and 14.4% in Koster. Thus, the Stu biomass changed much less from before to after the coppice than the roots, and it represented a higher belowground proportion for the genotype with the lower standing biomass (Koster). The root:shoot ratio exponentially decreased with basal area in a similar way for both genotypes before and after coppice (pre- and post-coppice, Fig. 6). As for Cr biomass the genotypic differences in root:shoot ratios were attributed to differences in the BA.

4. Discussion

4.1. Fine roots

The small reduction of Fr biomass observed during the growing season post-coppice (2012) is comparable with the lower Fr biomass observed after harvest of the aboveground biomass in an

Table 3
Aboveground (stems + branches) and belowground (stump + medium-sized + coarse roots) woody biomass from two 2-year and 4-year old poplar genotypes (Skado and Koster) grown on two former land-use types (cropland and pasture). The above- and belowground biomass components were estimated using allometric relations and diameter inventories. Leaf and fine root biomass were not included. Mean values (± standard error) are presented. DM = dry mass; Past. = former pasture; Cropl. = former cropland. No significant differences were found between genotypes or land-use types in the initial tree density (Tukey; $P < 0.05$).

Genotype	Land use	Initial density (trees m^{-2})	Tree mortality (%)		Aboveground (g DM tree^{-1})		Belowground (g DM tree^{-1})		Root:shoot ratio	
			2012	2014	2012	2014	2012	2014	2012	2014
Skado	Cropl.	0.767 (±0.03)	6.3	6.3	1562 (±32)	4100 (±96)	717 (±18)	1116 (±53)	0.46	0.27
	Past.	0.723 (±0.03)	24.8	24.3	1735 (±70)	4231 (±202)	782 (±29)	1140 (±59)	0.45	0.27
Koster	Cropl.	0.687 (±0.04)	18.0	19.0	765 (±44)	3269 (±132)	534 (±23)	1070 (±56)	0.70	0.33
	Past.	0.687 (±0.04)	17.6	23.1	1175 (±65)	3530 (±150)	670 (±29)	1132 (±58)	0.57	0.32

oak plantation (Ma et al., 2013). The higher Fr productivity post-coppice partially rejected our first hypothesis, and was in line with the higher aboveground productivity measured in 2012 (post-coppice) as compared to 2011 (Verlinden et al., submitted September 2014). This 46% increase in Fr productivity post-coppice could probably be explained by the higher precipitation (19% higher) and evapotranspiration (33% higher) in 2012 as compared to 2011 (Fig. 2). The increasing Fr mortality after the coppice of the aboveground biomass partially confirmed our first hypothesis, and validates the assumption of several SRWC models (Garten et al., 2011; Werner et al., 2012). These results contrast with the lack of change in Fr mortality after coppice observed in minirhizotrons studies (Dickmann et al., 1996; Dipesh and Schuler, 2013). The cumulated mortality was higher than the cumulated production beginning from autumn, when finer roots naturally die more after the peak of productivity. Apart from the increased Fr mortality, and as a consequence of the increasing C inputs into the soil, the coppice also might have negative effects on the soil C sequestration. For example, the removal of aboveground biomass changes the microclimate. The decomposition of the forest floor C is temporarily stimulated after harvest, because the soil becomes warmer and possibly wetter due to the reduced evapotranspiration (Piene and Vancleve, 1978). Moreover, the coppiced field site is more exposed to wind and to erosion. Experimental studies in timber plantations showed that soil C decreased with increasing harvest intensity (Nave et al., 2010).

The Fr biomass values were slightly higher than values reported for SRWC poplar on nutrient poorer soils in the same region (Al Afas et al., 2008). The absence of genotypic differences belowground has been also found for two other aboveground contrasting poplar genotypes in USA (Dickmann et al., 1996). The higher presence of weeds and the intensive weed management in the former pasture as compared to the former cropland caused a higher mortality of trees by mechanical and chemical treatments (Broeckx et al., 2012). The lower Wr biomass after coppice (2012) could be explained by the faster canopy closure of the poplars (higher leaf area index) and the lower weed presence after the coppice (Broeckx et al., submitted September 2014). The different root profiles observed in Fr and Wr was similar to the ones observed in native ecosystems, where tree roots show deeper rooting profiles than grass species (Jackson et al., 1996).

4.2. Coarse roots

The Cr biomass values found in our plantation (155–187 g DM m^{-2}) were lower than the values of 390–2980 g DM m^{-2} reported for older and less dense tree plantations (Puri et al., 1994; Tufekcioglu et al., 1998; Toenshoff et al., 2013). The low Cr biomass values could probably be attributed to the limited rooting depth, i.e. almost no Cr roots were found below 60 cm. We observed a shallow root system in both genotypes, and the water table was a strong determinant of the rooting system depth (Berhongaray, 2014) in line with the natural riparian habitat of poplars. Typically, poplar trees have relatively shallow but widespread root systems (Dobson and Moffat, 1999). As poplar is an opportunistic rooter, it does not produce roots at deep soil layers when there is sufficient water available or a high water table (Hallgren, 1989). The latter was the case at the site of this study; the average water table depth was 85 cm (Berhongaray, 2014). Since we used only one unique allometric equation to scale-up Cr, the genotypic differences in Cr are due to differences in the basal area frequency distribution, in the final planting density and in the mortality rate (Table 3). On average, Skado had significantly larger stem diameters than Koster (Verlinden et al., 2013a). Moreover, in genotype Koster we observed a high increment of Cr in the second rotation, as compared to Skado. This could be because Skado grew faster than Koster in the first rotation, and occupied the soil more rapidly. In the second rotation Skado had less space to grow, while Koster still had some soil to occupy.

The potential of SRWC to sequester C in the soil has been recently questioned by Walter et al. (2014). However, the belowground woody biomass (Stu + Cr + Mr) represents the second largest C pool of the SRWC system (Berhongaray, 2014). This long-term belowground biomass also contributed to the enhancement of the C sequestration along the four years of the plantation (Pacaldo et al., 2014). The value observed for the C sequestration (240 g C m^{-2}) was much higher than the 90 g C m^{-2} reported for an SRWC plantation in Canada (Arevalo et al., 2011). This might be due to the higher planting density at our site.

4.3. Root:shoot

Although the aboveground biomass for genotype Skado was 23% higher than for Koster, there were no differences in the total belowground biomass. Another study that compared aboveground contrasting genotypes also found that genotypes were less clearly contrasted belowground than aboveground (Dickmann et al., 1996). The root:shoot ratio exponentially decreased with basal area in a similar way for both genotypes before and after coppice (pre- and post-coppice, Fig. 6). This interesting observation rejected our second hypothesis of a change in the root:shoot ratio after a tree is converted from a single-stem to a multi-shoot system (i.e. from pre- to post-coppice). As for the Cr biomass the genotypic differences in root:shoot ratios were attributed to differences in the BA. For young Scots pines an increment of the root:shoot ratio with stem diameter increment was reported, in contrast to our findings (Xiao and Ceulemans, 2004). This could be explained by the fact that these evergreen trees were growing on poor forest soils. Similar to various other studies (reviewed by Mokany et al., 2006) we found that the root:shoot ratio increased with increasing aboveground biomass. Biomass allocation (to above- versus belowground) was not under strong genetic control, in contrast to some other studies that compared different poplar genotypes (King et al., 1999; Yin et al., 2005). In this study we compared, however, only two genotypes under non-limiting growth conditions.

4.4. Methodology used

In this study we used the technique of core sampling for the determination of Fr biomass, and tree excavation for the biomass estimations of Mr and Cr. The core sampling methodology is recommended for the sampling of uniformly distributed roots, such as for Fr biomass (Levillain et al., 2011). With increasing root diameters the (spatial) variability of the lateral root distribution also increases; so the sampling of an increasing amount of soil volume enables a better sampling of this belowground heterogeneity.

Our observations on the root:shoot ratio may also have differed from other studies because of the different definitions that are used. The distinction between below- and aboveground biomass was based on the arbitrary position of the ground surface. In some ecosystems, a considerable proportion of the roots occur above the ground surface and likewise, part of the stem biomass sometimes occurs below the soil surface (Mokany et al., 2006). There might be some disagreement about considering the 15 cm of Stu aboveground as a belowground component, but the Stu only represented 5–6% of the total tree biomass. The root:shoot ratio does not represent the total C allocation to the tree compartments, since it does not incorporate the considerable loss of C resulting from respiration and senescence (turnover). So, the root:shoot ratio only represents the net effects of carbon allocation. Although root:shoot ratios may only be rough indicators of physiological processes affecting C allocation, they are very valuable for providing estimates of belowground plant

biomass from aboveground biomass. For example, multiplying the biomass of the tree organs by its turnover and decomposition rates indicates that C allocation in trees strongly influences forest C cycling. Consequently a proper understanding of C allocation is an important issue in the context of best management practices for biomass production and C sequestration in the soil.

5. Conclusions

The coppice of the aboveground biomass resulted in a large Fr mortality and a tremendous input of C to the soil. The results obtained after coppice could be confounded with the tree ontogeny, and a control without coppicing at year 3 and 4 would have been useful. However, that experimental design was not possible as the plantation was treated as a commercial plantation with homogenous management in the whole area. Larger trees stored significant amount of C belowground with bigger root system, but bigger trees did not necessarily produce more fine roots. Both poplar genotypes only rooted in the upper 30 cm, and they showed relatively shallow, but widespread root systems. These results have implications for the design of C sequestration strategies.

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